

Measuring the evolution of facial 'expression' using multi-species FACS

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Highlights

- Facial Action Coding Systems (FACS) are useful tools for facial behaviour measurement
- FACS is objective, anatomically based and systematic
- FACS have been created to facilitate cross-species comparison
- Homology is indicated by stereotypy, physical and anatomical similarity, and presence across multiple species
- FACS can help determine homology of facial behaviour across species

Abstract

Darwin observed that form, and in his view, meaning, of facial behaviour (observable changes in the appearance of the face, often termed facial 'expression') is similar between a wide range of species and concluded that this must be due to a shared ancestral origin. Yet, as with all social behaviours, exactly how to define similarity and determine homology is debated. Facial behaviour is linked to specific facial muscle movements, so one important factor in determining homology is the anatomical basis of facial behaviours that appear similar in both appearance and social function. The Facial Action Coding System (FACS) was developed for the scientific

measurement of human facial behaviour and is based on individual facial muscle movements (Ekman and Friesen, 1978). FACS has since been modified for use with various non-human primate species (chimpanzees, macaques, hylobatids, orangutans) and domestic species (dogs, cats, horses). These FACS can be used to trace continuity of form in facial behaviour across species and build a better understanding of the evolution of facial communication in mammals.

Keywords: Facial expression; facial displays; facial behaviour; facial muscles; emotion; communication; primates; FACS

1. Introduction

The evolution of modern *Homo sapiens* is thought to have been accompanied by rapid cognitive and behavioural change equipping modern humans with many complex and unique traits (Tomasello, 2008). Some of the most complex and interesting aspects of human mind and behaviour are therefore unique to humans. Human language, for example, is not found in other species and is thus thought to have evolved fairly recently in the hominid lineage, possibly as recently as 50,000 years ago (e.g. Klein, 2017). Such uniqueness renders a comparative approach to some aspects of cognition and behaviour challenging, as scientists need to investigate the precursors to these traits without the option of examining clear, unambiguous counterparts in other extant primates. Human facial behaviour (observable changes in the appearance of the face, often termed facial 'expression'), in stark contrast, has an abundant array of similar phenomena (in both form and function) throughout the primate order and in other mammals (Waller and Micheletta, 2013). This broad continuity across species suggests that facial expression evolved long before the arrival of modern humans, and that human facial behaviours are rooted in evolutionarily ancient displays. In comparison to some other human

traits, scientists are therefore presented with a much easier task when trying to understand the evolutionary trajectory and function of facial behaviour.

Despite the excellent scientific opportunity presented by the existence of similar facial behaviour across species, there are still considerable theoretical and methodological challenges. The field of comparative facial communication research has attracted (and continues to attract) divergent theoretical approaches. First, scientists disagree on which criteria are needed to identify behaviours of shared descent, and thus how to identify unambiguous counterparts. Second, facial behaviours form part of a complex system of production (in the sender) and perception (in the receiver), in which we (the scientists) take part when we make observations. We argue that precise and objective methodology is therefore essential when studying facial behaviours in any species, to avoid biasing observations with our own categorical and emotional interpretation. For example, chimpanzee bared-teeth faces are perceived as more similar to human smiles when the underlying emotion is judged as similar, suggesting observers find it hard to distinguish meaning from form (Waller et al, 2007). Here, we review the development of objective anatomically based systems for the measurement of facial behaviour across species. The Facial Action Coding System (FACS) was originally developed for humans (Hjortsjo, 1969; Ekman et al., 2002; Ekman and Friesen, 1978) and has since been modified for use with several other animal species. We strongly advocate the use of these systems for comparative facial behaviour analysis and discuss how these can be used to better understand the evolution of facial behaviour.

2. How can we identify homologous facial behaviour?

“As scientists we want to know how justified our feelings of familiarity and understanding are and to what extent our impressions of oddity are based simply on anthropocentrism. To a biologist these questions translate into the question of whether a common heritage disposes us to understand some of the primate facial displays but not others, or whether

the perceived similarities and dissimilarities are only superficial and disappear on closer examination.” (Preuschoft and van Hooff, 1995, p. 122)

Since Darwin first noted the similarity of behaviour between species and speculated on common descent (Darwin, 1872), scientists have debated how best to identify and confirm the similarity that indicates common descent (homology). The first (and possibly most contentious) difficulty when trying to identify homology of facial behaviour, however, is agreeing on what is actually meant by facial behaviour, and which assumptions are made about the behaviour itself. The position one takes relates directly to which elements of the phenomenon under study are relevant, and which are not. Here, we define facial behaviour as observable facial movements associated with the typical behavioural repertoire of a species that potentially have communicative meaning to conspecifics. Similar common terms are facial signal or display (where evolution has acted on the behaviour to fix it as an adaptation for communication: e.g. Guilford and Dawkins, 1991). Similarly, we could use facial cue, where ‘cue’ refers to behaviours from which others can detect meaning but which have not been subject to natural selection for the explicit purpose of communication (e.g. Bradbury and Vehrencamp, 1998). However, such terms suggest there is evidence that the behaviour transfers information and is ‘received’ by another party. In the absence of data demonstrating this communicative function, such a term might be equally problematic. Others (such as Darwin, 1872) assume that an internal feeling state is being expressed through facial movements, and therefore use the term facial ‘expression’. We argue that such a term is unhelpful, despite being commonly used by scientists and lay people in common discourse. We do not deny that emotion *can* be associated with facial behaviour, but there is strong evidence that facial behaviours are often not associated with internal states, can be generated in multiple and polarised emotional contexts, and are often not generated during extreme emotional experience (e.g. Barrett, Adolphs, Martinez, Marsella and Pollak, 2019). Crucially, there is little direct evidence that changes in internal state are associated with facial behaviour in non-human animals, but scientists still regularly use the term facial ‘expression’ to refer to their facial behaviour (see Waller et al., 2017

and Fridlund 1994 for a discussion of this) . Therefore, despite widespread and dominant usage, here we avoid the term facial 'expression', and instead use the term facial behaviour. There is a risk that using different terms to refer to the same thing creates discontinuity within and between fields, but we hope that others follow suit in using more neutral terms to facilitate clarity about the phenomena under study.

A facial behaviour can be associated with multiple layers of behaviour and experience (see Figure 1), some of which may be good criteria for homology, and some of which may not. A facial behaviour is typically associated with several proximate processes: facial muscle action, physiological changes in neural and/or somatic processes, and changes in feeling state (e.g. emotion, motivation). These processes can result in an observable facial appearance change, which may or may not be meaningful to others (have signal value), and which may or may not have an impact on others in social interaction. While most scientists agree that facial behaviours can be associated with some or all of these phenomena, they disagree on which are necessary for the definition of facial behaviour, which of these are the most important aspects to identify homology, and the specific role these processes have in defining the meaning of a facial behaviour. For example, the change in feeling state could act as a mechanism for production (e.g. facial feedback hypothesis: Strack et al., 1988, but see Noah, Schul and Mayo, 2018), or could be a meaningful *outcome* of production resulting from the social interaction. The relationship between these layers is also debated. Specific facial movements have also been proposed to have proximate function. For example, Lee et al (2014) argue that eye widening in fear behaviours functions to optimise stimulus detection, whereas the eye narrowing in disgust (antithetical to fear) functions to optimise visual discrimination.

Preuschoft and van Hooff (1995) examined the most commonly used criteria for behavioural homology in the classic ethological literature (Lorenz, 1950; Tinbergen, 1962) and discussed whether primate facial behaviours or displays meet these criteria, and how best to test this. Criterion 1 states that only stereotyped forms of behaviour can be homologised due to the need for communicatory signals to be unambiguous to receivers. The authors argued that while primate facial behaviours tend to be stereotyped and thus meet this criterion, experimental

data are needed to confirm how and whether such signals are recognised by and elicit responses from others. Therefore, the authors emphasised the importance of analysing responses from the receiver (receiver psychology: Guilford and Dawkins, 1991) in determining whether the facial behaviour is in fact stereotyped, thus avoiding using our own subjective judgements on whether a display appears stereotyped.

Criterion 2 specifies that to be considered homologous, facial behaviours need to resemble each other in many individual elements of the face, and that the likelihood of homology increases with complexity. At the time of writing, there were no FACS available for use with species other than humans, but the authors argued that FACS could be a useful method to determine whether the components of facial behaviours are morphologically similar. An additional advantage of using FACS is that it forces scientists to examine the details of facial behaviours rather than the whole, which encourages a more objective and precise measurement of facial features. In social interaction it may be advantageous for us to see faces as wholes, allowing us to process them quickly (e.g. Richler et al., 2009) and more accurately (e.g. Van Belle et al., 2010), but this is not necessarily helpful when examining faces scientifically to measure the details.

Criterion 3 specifies that facial behaviours may be homologous when they are accomplished by homologous body structures. i.e. the facial elements (nose, eyes, ears and mouth), and the underlying facial musculature. The authors argued that while the basic facial elements and facial musculature are undisputedly homologous, there was (at the time) doubt about whether facial actions could be linked to specific facial movements: “homologizing of facial displays on the basis of the underlying structures of muscles implies that these structures are sufficiently clearly delimited and that an unambiguous matching of facial actions to activation states of identifiable muscles is possible. This is far from granted.” (Preuschoft and van Hooff, 1995). However, recent extensive anatomical work has confirmed the link between facial muscles and facial movement in two species or primate (Waller et al., 2006), and the development of several FACS systems also supports a direct link (e.g. Parr et al., 2010; Vick et al., 2007). Thus, confirming direct correspondence between facial muscles and facial

movements is now possible in many species of primate. The authors, however, went on to argue that even if different muscles are involved in similar behaviours this does not necessarily imply a lack of homology. Their reasoning was that facial muscles are not always well differentiated from each other and bundles of fibres can become dislocated during evolution as face shapes change, perhaps taking on the function of older muscles. While this may be possible, the growing literature on primate facial musculature suggests that the facial muscles and their insertion points and attachments are rather more conserved than Preuschoft and van Hooff (1995) cautioned at the time of writing (Burrows, 2008). Hence, we argue that demonstration of similar underlying musculature of facial behaviours should be a necessary criterion for homology until the anatomical evidence demonstrates more divergence than suggested currently.

Related to the homology of underlying facial musculature, is whether activation of these structures are underpinned by similar neural substrates. Understanding the manner and extent of control over facial muscles is crucial to understanding whether individuals can use them voluntarily and flexibly, which might differ between species even if facial behaviours have the same muscular correlates. Fine-grained control of facial muscles likely increases as complexity of facial behaviour increases. For example, the human tongue has a higher proportion of slow-twitch muscle fibres compared to fast-twitch fibres than rhesus macaques (Sanders et al, 2013). These two types of muscle fibre have properties suggesting they are specialised for different functions. Slow-twitch fibres are more resistant to fatigue and generally involved in activities requiring precise control of weak forces. Similarly, some facial muscles in the human face also have a higher proportion of slow-twitch myosin than rhesus macaques and chimpanzees (Burrows et al, 2014), suggesting that these muscles can be used in a slower and more precise manner. It is possible, therefore, that a higher proportion of slow-twitch fibres is also suggestive of greater volitional control of a muscle. The volume of the facial nuclei of the brainstem is also greater in great apes and humans in comparison to monkeys, suggesting that these species have greater motor control of facial muscles generally (Sherwood et al., 2005), but we do not know how this might relate specifically to different facial behaviours.

The relationship between muscles, and how these combinations are activated, is a crucial aspect of facial behaviour complexity and may also differ between species (even when the basic muscular underpinning of behaviours appear superficially similar). Indeed, many primate facial behaviours are not at all static and fixed, and instead manifest as graded and dynamic sequences (e.g. Parr et al., 2005). A better understanding of the neural basis of facial muscle activation across species is needed to explore this. Human facial muscles appear to group as modules in head/neck anatomy, with the physical connections between structures being stronger or weaker depending on function (Esteve-Altava et al., 2015). but how this arrangements differs between species is currently unknown. FACS (see below) could be used, however, to document which muscles can be used independently, and which always co-occur. Therefore, a facial behaviour might have a similar muscular basis across species, but might still differ in terms of the flexibility of production within the facial behaviour (Clark et al. in review).

Preuschoft and van Hooff (1995) set a fourth criterion for homology of facial behaviours, arguing that the existence of intermediate displays can testify to phylogenetic continuity: “a tightly knit sequence of small steps of changes strongly suggests homology”. Ideally this would be present in the fossil record, but in the absence of such data, evidence can come from extant related species or ontogenetic transitions within the same species. For example, lip smacking and silent bared-teeth displays seem to form a continuum across old world monkeys, with an intermediate teeth chattering display (van Hooff, 1967). However, again the authors cautioned against using this criterion too strictly as “no extant species can be regarded as ‘frozen’ ancestors of other living species” (Preuschoft and van Hooff, 1995). In criterion 5 the authors stated that the presence of similar displays in a large number of related species suggests homology. Ubiquitous facial behaviours such as bared-teeth displays and relaxed open-mouth displays, therefore, should be integrated into an established phylogenetic tree to understand the temporal sequences and relationships. Such an approach has been applied successfully to trace the evolution of laughter vocalisations across great apes (Davila-Ross et al., 2009), and FACS can now be used to adopt this approach with facial behaviours (see below).

Finally, Preuschoft and van Hooff (1995) examined a sixth criterion for homology, that association with the same motivational complex may indicate homology. In facial behaviour, this could relate to the feeling state (e.g. emotion, motivation) that is often assumed to accompany the facial behaviour (Figure 1). The authors argued, and we concur, that there are serious limitations of the applicability of this criterion. First, the facial behaviour can become emancipated (*sensu* Tinbergen, 1952) from its original motivational complex and shift into another motivational complex. Indeed, shift in underlying motivation is a well established element in the process of ritualisation where a behaviour becomes stereotyped and transformed into a communicative signal (Tinbergen, 1952). Preuschoft (1992) evidenced this point clearly, with data demonstrating that functional differences in use of the morphologically similar silent bared-teeth display across macaque species are related to differences in species social style. The silent bared-teeth has a submissive function in the most despotic species of macaque, ranging to an affiliative function in the most egalitarian species. Thus, the underlying motivation and emotion of these similar facial behaviours is unlikely to be the same, rendering similarity of emotion or motivation an unreliable indicator of homology. Similarly, facial behaviour can have different meaning depending on context. For example, in humans, prototypical basic emotional facial behaviours can take on different meanings depending on how they are paired with different body postures (Aviezer et al., 2012). Emotion, however, is clearly a focus of interest for many researchers interested in facial behaviour. Bard (2008) argues that “although the morphology of the face differs, the focus on ‘felt’ emotion links the chimpanzee playface with the human smile”. Therefore, the authors are less interested in whether the behaviours share the same historical ancestry, but instead on whether the species share similar emotions. We argue, however, that the difficulty in assessing the subjective state of other species, particularly if behavioural indicators are different, makes this a contentious issue. This is not to say that emotion is not an interesting part of the facial behaviour and unworthy of attention, but that its inclusion can confuse discussions when identification of homology is the goal.

In sum, and following on from the classic work of Preuschoft and van Hooff (1995), the criteria we endorse as good criteria for assessing the homology of facial behaviour are as follows:

- A. Stereotyped and identifiable (as defined by the recognition of conspecifics).
- B. Similarity of multiple elements (e.g. FACS action units).
- C. Homology of underlying facial musculature (and neural substrates).
- D. Presence in a large number of related species (where form and function can be understood in relation to phylogeny).

We argue that adherence to these principles for the identification of homology is important to measure the continuity and evolution of facial behaviour across species.

3. What is FACS?

The investigation of human facial non-verbal communication has been greatly facilitated and standardised by the development of the Facial Action Coding System (FACS: Ekman et al., 2002; Ekman and Friesen, 1978). Prior to this, the human facial behaviour field was reliant on more subjective methods and did not have a systematic way to assess the muscular components of facial behaviour (and thus help determine homology, see above). Duchenne de Boulogne (1862), however, was the first scientist to pursue a strongly anatomical approach to human facial behaviour, and conducted a series of electrical stimulation studies to try and link facial muscles to specific behaviours. Duchenne wanted to understand how facial landmarks shaped facial behaviours, and map the connection between the contraction of individual facial muscles and observable facial displays. Building on this seminal work, Hjortsjo (1970) was the first to try and use an understanding of the relationship between facial muscle contraction and facial movements to develop a usable coding scheme for research. Hjortso (1970) attempted to identify the smallest independent units of muscle movements in the face, and use numbered codes to refer to their appearance changes on the face. This approach set the scene for FACS development.

Following directly from the anatomical work of Duchenne (1862) and Hjortsjo (1970), FACS identifies the appearance changes related to facial movements and aims to identify individual muscle contractions, focussing not on the expression of emotions but on the production of spontaneous facial movements. For example, FACS is able to compare facial behaviours objectively across individuals regardless of the inherent variability in the surface morphology of faces, e.g., bone structure, fatty deposits, skin texture, and individual muscle variations (Waller et al., 2008b, 2007). There is some debate, however, about the underlying assumptions of FACS. Some studies suggest that the facial musculature is not consistent between individuals, muscles sometimes differing in term of presence, size and symmetry of the muscles (McAlister et al., 1998; Pessa et al., 1998; Waller et al., 2008b) as well as in fatty deposit and in neural supply (Ekman, 1980). Neuropsychological studies have also shown a greater involvement of the left half of the face in the expression of facial behaviours, leading to asymmetrical displays of emotion (Borod et al., 1997). Moreover, some people have greater facial flexibility and/or control over their facial muscles, allowing for the production or suppression of more facial movements (Cole et al., 1996). However, the success with which FACS can be applied suggests that these issues do not affect the application of FACS in any great depth.

FACS uses numbers to refer to the appearance changes associated with 33 facial muscle contractions (Action Units [AUs]) and 25 more general head/eye movements (Action Descriptors [ADs]). Most AUs refer to the contraction of single muscles, but some muscles always co-occur, or are capable of producing different movements. Thus, the correspondence between facial muscles and movements is not always direct. It presents each AU in terms of underlying musculature (location and direction of action), appearance changes (multiple cues for identifying AUs), reference for AUs (subtle differences between AU combinations), how to do the AU (voluntary production of AU in isolation), and intensity scoring for the AU (criteria for coding decisions). Because the system is based on the premise that muscles that vary only slightly within species (although this is largely an untested assumption), FACS can compare

facial movements regardless of superficial individual differences in other aspects of facial anatomy, such as hair covering, facial coloration, bone structure, etc. This latter characteristic also makes FACS ideal for modification across species. Figure 2 gives an overview of the muscle movements underlying FACS AUs in various species. The development of such a comprehensive coding system with the common language of AUs, with numerical codes and neutral labelling, has enabled researchers across a wide variety of sub-disciplines, often with diverging theoretical positions, to communicate and evaluate findings using a common language (see Ekman and Rosenberg, 1997). Moreover, the FACS method is particularly well suited to comparative studies (cross-cultural and cross-species) as it provides clear descriptions for the identification of each AU, listing various appearance changes (movement of facial landmarks, changes to the shape of facial features) that can be directly compared. FACS has even been used to try and describe the facial movements depicted on archaeological material culture (Samson and Waller, 2010). In sum, FACS has become the most widely used coding system in facial behaviour research, and requires training and certification to be used.

Since its creation, FACS has been used extensively in research (the original 1978 manual is cited by over 1025 articles; Google Scholar search in March 2019) and has been adapted for the study of facial displays of primary emotions (EMFACS: Friesen and Ekman, 1983) and for infants (BabyFACS: Oster, 2006), allowing researchers to investigate the facial behaviour of pre-linguistic infants (e.g. Longfier et al., 2016; Soussignan et al., 2018). FACS offers great flexibility for use in scientific research, and is largely atheoretical in the sense that it is purely a methodological tool. FACS can be used to code occurrences of AU/ADs (i.e. frequencies of each AU/AD: Galati et al., 2003), duration of AU/ADs (i.e. for how long was each AU/AD produced: Reed et al., 2012), and intensities, using either the full 5-point scale presented in the manual or any suited adaptation (i.e., small vs big intensity of movement; small vs intermediate vs max intensity). Moreover, FACS can also be used to code for specific AUs of interest, identified by the researchers based on previous literature or conceptualisation (Schmidt et al., 2009) or to code for all facial movements produced, using a bottom-up approach (Julle-Danière et al., in review).

As such, FACS has been used extensively in the study of facial behaviour of emotion (e.g. Keltner, 1996) and helps standardise data and stimuli for cross-cultural studies (e.g. Crivelli et al., 2017). This methodology also allowed for the creation of computerised stimuli or avatars posing genuine facial behaviours (Jack et al., 2016), or for the development of automated analysis of facial movements (Lien et al., 1998). More specifically, the development of EMFACS has been critical for developing automated coding systems (Lien et al., 2000; McDuff et al., 2016). However, it is important to note that FACS in itself is atheoretical, and how it is applied matters. The AU profiles of the prototypes of the six basic emotions published along with the human FACS (FACS Investigators Guide: Ekman et al, 2002) are used extensively as stimuli in research, but the typicality and relevance of these behaviours across cultures has been questioned (Jack, 2013; Barrett et al., 2019). Instead, we advocate using FACS simply as a tool to measure the production of facial behaviour in detail and objectively.

4. The development of Animal FACS

FACS has been modified for use with non-human species to facilitate objective facial behaviour measurement. However, there are important assumptions in this endeavour that should be taken into account. The human FACS is based on the assumption that what can be observed by a scientist is similar to what is perceived during human-human social interaction. Thus, the units of FACS (AUs) are assumed to be reasonable units of human perception. This makes sense when investigating human-human interaction as there is likely some level of correspondence between production and perception in human facial behaviour. However, when transferring the system to non-human animals this assumption may be less valid if the visual systems of other animals differ in what they can and cannot perceive. Caution must be taken therefore, and it is even more important that data is generated to confirm what animals do and do not respond to.

Adapting the original Human FACS for animals has followed a standardised process regardless of species. First, analysis of the facial musculature is conducted: the presence, size, and structure of facial muscles have been recorded through dissection (e.g. Burrows et al.,

2009, 2006) or through review of the existing literature if available (e.g. Caeiro et al., 2013; Waller et al., 2012). The facial muscles are compared with the facial musculature of other species to identify potential similarities and differences between species. Second, the surface movements of individual muscles are demonstrated using intramuscular stimulation techniques (Waller et al., 2008b, 2006). Third, the contraction of specific muscles is identified from video footage of spontaneous behaviour, and the surface appearance changes are described and compared in detail for documentation in the training manuals (e.g. www.animalfacs.com). Some FACS systems have been adapted from the Human FACS without following this 3-step procedure: the GibbonFACS (Waller et al., 2012), DogFACS (Waller et al., 2013), and EquiFACS (Wathan et al., 2015) were developed based on dissection and observation of spontaneous behaviours only. For ethical reasons, intramuscular stimulation (step 2) is avoided unless there is the opportunity to use an existing planned procedure under anaesthesia for the procedure (see Vick et al., 2006; Waller et al., 2008a). Intramuscular stimulation does provide additional information but is not essential.

To date, FACS has been modified for use with chimpanzees [*Pan troglodytes*: ChimpFACS (Vick et al., 2007)], rhesus macaques [*Macaca mulatta*: MaqFACS (Parr et al., 2010)], gibbons [Hylobatids, GibbonFACS (Waller et al., 2012)], orangutans [*Pongo* spp: OrangFACS (Caeiro et al., 2013)], dogs [*Canis familiaris*: DogFACS (Waller et al., 2013)], cats [*Felis catus*: CatFACS (Caeiro et al., 2017a)], and horses [*Equus caballus*: EquiFACS (Wathan et al., 2015)]. FACS has not yet been developed for rodents, but given the use of these species in biomedical research such developments should be a priority for future work. Each FACS system is based on the human FACS, so that individual movements can be directly compared between species. The development process itself, therefore, is highly informative because the process can reveal how similar the target species is (in terms of the capacity for facial movement) to the previous species under study. The eight species already used for FACS development share a minimum of 47% of their facial muscles (when using humans as a reference). The primate species present the highest similarities with humans in the presence of

muscles (97%), followed by the dog (67%), the horse (53%), and finally the cat (47%; see Table 1). However, even when muscles are shared, it does not necessarily follow that the movement is present. For example, primates share between 47% (chimpanzees and macaques) and 62% (gibbons) of facial movements with humans (despite sharing 97% of facial muscles) and dogs share 38% of facial movements with humans (despite sharing 67% of facial muscles, see Table 1). Thus the correspondence between muscle presence and muscle movements is not direct, some muscles can produce multiple movements, and some are rarely used (if at all). These systems have, however, allowed researchers to make objective assessments of homology between species (Parr et al., 2007) and to observe facial behaviours in greater detail than previous methodologies (Vick and Paukner, 2010). Following the original FACS requirements, all species-specific FACS necessitate training and certification to be used in research (e.g. www.animalfacs.com).

5. Applications of Animal FACS

Despite the increase in the number of FACS systems available, there are relatively few studies using this tool to answer questions about the evolution and function of facial behaviours. However, the studies that are available demonstrate how FACS can be a powerful tool to inform us about 1) the phylogenetic link between the facial behaviours of humans and other animals, 2) the cognitive mechanisms underpinning the production and perception of facial behaviours, and 3) the social and ecological correlates of facial behaviours.

Phylogeny. The development of a FACS system for chimpanzees (Vick et al., 2007) allowed the first comparison between human and nonhuman primate facial behaviour, based on objective anatomically based measures (Parr et al., 2007). The authors FACS-coded a large database of over 250 facial behaviour images from approximately 100 chimpanzees, resulting in a series of AUs characterising each facial display in the database. This detailed morphology of facial behaviours was subjected to a discriminant function analysis (DFA) to see if the labels

commonly used to describe chimpanzees' facial displays (e.g. bared-teeth display, play face, pant-hoot face etc.) could be used to classify the FACS-coded behaviours. The results revealed that FACS-coded behaviours could be matched to the existing labels consistently, validating ChimpFACS as a reliable method to describe chimpanzees' facial behaviours. The FACS analysis also revealed important variations that would have been missed by the use of relatively subjective labels such as bared-teeth or play face. The authors were able to identify movement combinations characteristic of each facial display, providing an objective, reliable and reproducible measure of what chimpanzees' facial behaviours actually look like. Since the same codes are used in all FACS system, a simple but unbiased method could be used to compare chimpanzee and human facial behaviours, going beyond subjective morphological descriptions. Human and chimpanzee facial behaviours were FACS-coded and grouped as potential homologues on a muscular basis, that is, according to the number of shared AUs. More recent work using a similar approach supported these findings when investigating the form of chimpanzee open-mouth faces (Davila-Ross et al., 2015). FACS was also used to quantify and compare responses to stimuli designed to elicit different emotional responses and levels of arousal in dogs and humans (Caeiro et al., 2017b). While dogs displayed distinctive facial movements in response to fearful, positive anticipation, and happiness contexts, the specific movements differed between dogs and humans. This suggest that despite a relatively similar morphology and long history of co-existence and mutual social interactions, facial behaviours are not homologous in these species.

To our knowledge, these are so far the only studies using FACS to identify possible homologies in facial behaviours. Since FACS is readily available for other nonhuman primates, this work could easily be replicated with other species to further our understanding of the evolution of human facial behaviours.

Domestication. FACS is available for domesticated species such as cats, dogs, and horses. Beyond implications for applied fields such as veterinary medicine, these systems allow researchers to address fundamental questions regarding the domestication process from a new angle. For example, the main hypothesis regarding wolves' domestication is that by tolerating

the proximity of humans to take advantage of the resources this afforded, wolves underwent a process of self-domestication (Coppinger, 2001). In which case, the physical features and behaviours seen in dogs today could be a consequence of selection against aggression. However, it is also possible that animals who displayed paedomorphic traits were preferentially selected by humans. Selection from rehoming shelters can be used as a model for this process, and DogFACS can be used to measure paedomorphic facial behaviours. For example, AU101 (inner brow raiser) results in the increase of the height and overall size of the eye, which is one of the most apparent paedomorphic trait on the face. Dogs who produced higher frequencies of this specific movement were adopted more quickly from rehoming shelters, suggesting that dogs might have evolved to manipulate our preference for paedomorphic traits (Waller et al., 2013). In this study, other behaviours such as tail-wagging and close proximity were not particularly good predictors of rehoming speed. This contrasts with a similar study using CatFACS, where facial movements were not associated with rehoming speed but affiliative behaviours such as rubbing were (Caeiro et al., 2017), highlighting how different selection pressures have been applied to the ancestors of our companion animals. The AU101 movement in dogs seems to have been accompanied by changes in the facial anatomy of dogs, demonstrating an evolutionary convergence from ancestral wolves (Kaminski et al 2019). Dissections showed that dogs have facial muscles underpinning AU101 that are not present (or variably present) in wolves, suggesting that the selection pressure to appear appealing to humans has acted on the soft tissues.

Cognition. FACS has also been used in studies to try and elucidate the cognitive properties underlying the perception and production of facial behaviour. For perception, FACS is used to standardise the stimuli presented to the animals and see how facial components of behaviours relate to performance. In a series of experiments using standardised avatar stimuli, created with ChimpFACS, chimpanzees were able to discriminate between a number of prototypical facial behaviours in a match-to-sample task (Parr et al., 2008). While this can be achieved without the use of a FACS system, follow-up analyses using FACS data in a multidimensional scaling analysis allowed the researchers to examine with precision the specific

morphological features allowing chimpanzees to discriminate the different facial behaviours. For example, AU26 (jaw drop) seemed to be important to differentiate pant-hoots from pouts and whimpers, despite all facial behaviours sharing AU22 (lip funneler). Screams and bared-teeth faces were easily distinguished by chimpanzees, apparently thanks to AU27 (mouth stretch) which is the only AU present in scream faces but not bared-teeth faces. These key features were then used to test the ability of chimpanzees to match full prototypical displays (e.g. bared-teeth, AU10+12+16) to displays featuring only one of the individual components of the display. The results of this experiment confirmed that at least one AU was more salient than the others for each facial behaviour. Although configural information was important as well, as evidenced by a strong inversion effect, the use of FACS revealed that component movements are highly important for receivers of facial behaviours, especially when there is a strong overlap overall (e.g. between scream faces, AU10+12+16+27, and bared-teeth faces, AU10+12+16). Similarly, Parr and Heintz (2009) used MaqFACS to interpret the error patterns in facial behaviour processing tasks in rhesus macaques, and found that specific AUs could be responsible for the animals' discrimination between behaviours. Micheletta and colleagues (2015) then used MaqFACS to analyse error patterns in facial behaviour processing tasks with crested macaques (*Macaca nigra*). Interestingly, in contrast to the rhesus macaques, overall similarity (measured by MaqFACS) did not correlate with performances and the authors concluded that functional similarities between facial behaviours are more likely to influence the animals' perception of similarity.

FACS has also been used in studies of primate facial behaviour production. Whether the production of communication is sensitive to the attentional stance of a conspecific (or human experimenter) has been proposed as an indication of intentionality (Leavens et al., 2004). Others have suggested that there are other lower level explanations for this phenomenon, such as production being responsive to subtle social context (Liebal et al., 2014), but nevertheless this marker is commonly employed in the primate communication literature (particularly in relation to gesture). FACS has now been used to examine subtle differences in production in relation to visual attention in orangutans and gibbons. Orangutans produced more complex

(more AUs) and more intense (inclusion of AU27, mouth stretch) playfaces when a play partner was facing them during social play, regardless of play intensity (Waller et al., 2015). Similarly, gibbons produced longer lasting facial behaviours when facing another individual during spontaneous social interaction (Scheider et al., 2016). Such studies are crucial to determine whether the properties of primate communication differ depending on the form of communication (e.g. facial, gestural or vocal). Indeed, scientists rely on these comparisons to explore the likely primate precursors to human language (Slocombe et al., 2011). One study has also examined the production of domestic dog facial behaviour using DogFACS. In an experimental study, dogs produced significantly more facial movements when a human demonstrator was attending to them than when she was not (Kaminski et al., 2017). As with the primate data, this demonstrates that dogs can be sensitive to attentional state when producing facial behaviours, suggesting that facial behaviours are not just inflexible and involuntary displays of emotional states. Interestingly, as the visual attention is here from a human and not a conspecific, the findings also have implications for the impact of domestication on how dogs might use their facial behaviours specifically with humans.

Social and ecological correlates of facial behaviours. FACS has been used fruitfully in comparative studies to evaluate the social and ecological factors acting as potential selection pressures shaping facial mobility. In the first large-scale comparative study, Dobson used FACS to measure facial mobility in 12 nonhuman primate species, and showed that body mass explained much of the variance in facial mobility, when controlling for phylogeny (Dobson, 2009a). Specifically, larger species tend to produce a greater number of unique movements. This relationship might be the result of a better visual acuity in larger species (Kiltie, 2000), implying that while the advantages of being able to produce a large variety of often subtle facial movements could be advantageous for larger species, it may be negligible for smaller ones. It is possible that smaller species rely on other forms of communication instead, but this is still to be tested.

This allometric relationship between facial mobility and body size is not perfect, as some species strongly deviate from the general pattern. Given the importance of social and ecological

factors in shaping socio-cognitive and communication skills (Byrne, 1996; Byrne and Whiten, 1988; Freeberg et al., 2012; Humphrey, 1976), Dobson (2009b) hypothesised that these factors could also contribute to explaining variations in facial mobility between species. Phylogenetically informed correlations, controlling for body size, suggested that terrestrial species tend to produce a great diversity of facial movement, which could be the result of limited visibility in the canopy (Dobson, 2009b). Facial mobility also increased with group size, a pattern that has been observed for vocalisations in numerous species, including primates (McComb and Semple, 2005), birds (Freeberg, 2006), rodents (Blumstein and Armitage, 1997) and bats (Wilkinson, 2003). As group size increases, an increased repertoire of facial movements might be advantageous to navigate a complex social environment and maintain group cohesion (Freeberg et al., 2012).

Group size, however, does not seem to be the only factor affecting facial mobility. Within closely related species, factors such as social tolerance and the strength of pair bonds have also been investigated. In macaques, different species occupy different positions on a continuum of social tolerance (Thierry, 2007). The number of facial displays in a species repertoire have been found to positively correlate to two measures of social tolerance: conciliatory tendency and rates of counter-aggression (while controlling for phylogeny: Dobson, 2012). Species characterised by higher degrees of social tolerance face greater uncertainty in the outcome of social interactions, and an increased repertoire of facial displays might constitute a powerful tool for social negotiations in this context. However, it should be noted that this facial repertoire size was not measured with FACS, and a more thorough investigation might reveal different results. Using GibbonFACS, Scheider et al. (2014) described three properties of the facial behaviours of five hylobatids: the rate of facial behaviours, the size of the facial behaviour repertoire, and the diversity of behaviours. Siamangs (*Symphalangus*) displayed a higher rate of production and a higher diversity of facial movements, compared to *Hylobates* and *Nomascus* species, but the differences were not related to group-size or the level of monogamy (Scheider et al., 2014). Although surprising given previous findings (Dobson, 2009b), the lack of statistically significant relationship might be the result of the limited variability in group-size for

the species under investigation. Building on this work, a more recent study used GibbonFACS to expand the known repertoire of facial behaviours in hylobatids, and test the relationship between the strength of pair-bond and facial expressiveness, measured as repertoire use, repertoire size, and facial behaviour synchrony (Florkiewicz et al., 2018). Facial behaviour synchrony was correlated to pair-bond strength, leading to the conclusion that in these species, facial behaviours are an important way of maintaining pair-bonds via close range visual communication.

6. Conclusion and future directions

Comparative analysis of facial behaviour across species attracts different methods and theoretical approaches. Following on from the seminal work of Preuschoft and van Hooff (1995), we argue that to be considered homologous across species, and therefore similar through common descent, facial behaviours need to demonstrate the following: a stereotyped and recognisable form (as defined by the recognition of conspecifics), similarity of multiple elements, homology of underlying facial musculature and presence in a large number of related species. FACS systems are a useful tool to assess these criteria as they capture the component parts of facial behaviours (based on muscle movements) and can be used across multiple species using the same anatomically based terminology. So far we have developed FACS for a range of species, but we need to increase the number of FACS system in order to conduct large scale phylogenetic analyses and for a better representation of primate diversity in comparative studies. For example, there are currently no FACS systems for *Papionini*, *Calitrichidae*, *Cebidae* or *Lemuridae*. Existing comparative studies are limited to closely related species displaying minimal morphological variability, such as the macaques and hylobatids. Extending FACS development to more species will allow more thorough investigations on the evolutionary pathways for facial behaviours, but also allow us to address important questions related to the evolution of communicative complexity, with potential implications for the evolution of human communication. We also need to develop research programs investigating the development of

facial behaviours. There are currently no existing studies using FACS to determine how and when facial behaviours emerge during development across species, which could yield crucial data about the factors determining their production.

One important limitation of FACS is how to use it to quantify and summarise the expressivity of an individual or species. The strength of FACS is in its flexibility, scientists can use it in many different ways as it is purely a descriptive tool, but this is also a weakness if we do not fully exploit the potential of FACS. Current studies are limited to counting the number of AUs or combinations of AUs, which is arguably a poor proxy for the complexity of movement that a face is capable of. Facial behaviours are dynamic, blended and merged, and while FACS can go some way to describing these features, there is currently no existing method to capture these aspects of facial behaviours in a usable metric. We could learn a great deal from the study of vocalisations, where statistical innovations have been put in place to investigate the complexity of call sequences (Kershenbaum et al., 2016; Weiss et al., 2014). We could also adopt approaches used in human facial behaviour research where the signal value of the face, in terms of which AUs are 'received' and which ones are not, is argued to be paramount in determining diagnostic features (Jack and Schyns, 2017). Crucially, however, such an approach relies on testing the categorical responses of the observer (e.g. Yu et al., 2012) which requires significant training in nonhuman primates. Cognitive training and testing primates is possible and effective but requires time and resource investment, and access to a wide range of species in captivity. Such innovations have paved the way for ground-breaking advances, however, and the study of facial behaviour should follow these trajectories and use increasingly objective, standardised and experimental methods.

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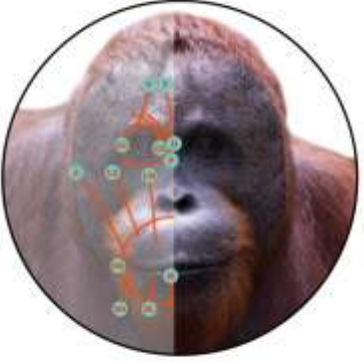
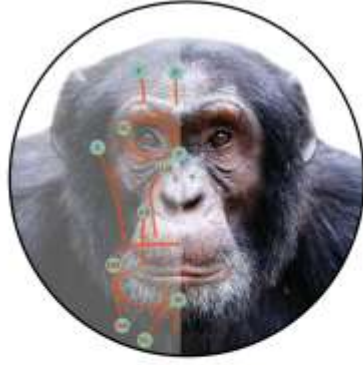
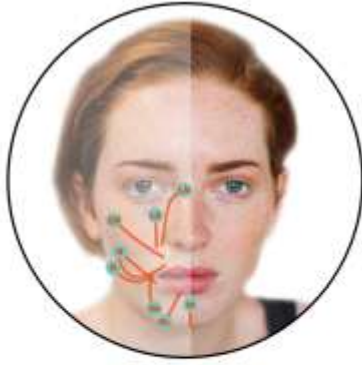
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Figure Captions

Figure 1. The multiple elements of a facial behaviour. Photo by Ugiek Giyarto ([Macaca Nigra Project](#)).



Figure 2. Muscle maps for the different animal FACS. Circles show muscle origins, and lines show attachment points. Movements go from the attachment point toward the origin. B: buccinator; CA: caninus; CS: corrugator supercillii; D: depressor; DA: depressor anguli oris; DL: depressor labii inferioris; F: frontalis; IL: incisivii labii; LA: levator anguli oculi medialis; LF: levator annuli oris fascialis; LL: levator labii maxilaris; LN: levator labii superioris alaeque nasi; LO: levator anguli oris; LS: levator labii superioris; LT: lateralis nasi; M: mentalis; NA: nasalis; OC: orbicularis oculi; OR: orbicularis oris; P: procerus; R: risorius; RO: retractor anguli oculi lateralis; ZM: zygomatus minor ; Z: zygomatus major. For clarity, ear movements and Platysma are not shown. See www.animalfac.com for details. Credits: Human photo by Raj Rana; Chimpanzee photo by Ronald Woan (CC BY-NC 2.0); Orang-utan photo by Ray Muzyka (CC BY-NC-SA 2.0); Gibbon photo by Phil Greaves; Macaque photo by Cristian Ungureanu; Dog photo by Leonides Ruvalcabar; Cat photo by Manja Vitolic; Horse photo by Cristofer Jeschke.



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Tables

Table 1. Identified AUs in humans, chimpanzees, macaques, gibbons, orangutans, dogs, cats, and horses, according to the underlying musculature

AU	Muscle	Abbr. in figure	Human FACS	Chimp FACS	Maq FACS	Gibbon FACS	Orang FACS	DogFACS	CatFACS	EquiFACS
AU1 Inner Brow Raiser	Frontalis (medial)	F	✓	x	x	x	x	✓ AU101 (Levator anguli oculi medialis)	a	✓ AU101 (Levator anguli oculi medialis)
AU2 Outer Brow Raiser	Frontalis (lateral)	F	✓	x	x	x	x	x	a	a
AU 1+2 Brow Raiser	Frontalis	F	✓	✓	✓	✓	✓	x	a	a
AU4 Brow Lowerer	Procerus, depressor and corrugator supercilii	P, D, CS	✓	x	x	x	✓	a	a	a
AU41 Glabella Lowerer	Procerus	P	✓	x	✓	✓	x	a	a	a
AU5 Upper Lid Raiser	Orbicularis oculi	OC	✓	x	x	✓	x	x	✓	✓
AU6 Cheek Raiser	Orbicularis oculi	OC	✓	✓	✓	✓	✓	✓	a	a
AU7 Lid Tightener	Orbicularis oculi	OC	✓	x	x	✓	x	✓	a	a
AU8 Lips toward each other	Orbicularis oris	OR	✓	x	✓	x	x	a	a	a
AU9 Nose Wrinkler	Levator labii superioris alaeque nasi	LN	✓	✓	✓	✓	✓	✓ AU109+110 (Levator nasolabialis,	✓ AU109+110 (Levator nasolabialis,	a

AU10 Upper Lip Raiser	Levator labii superioris	LS	✓	✓	✓	✓	✓	caninus, levator labii maxillaris)	caninus, levator labii maxillaris, lateralis nasi)	✓
AU11 Nasolabial Furrow Deepener	Zygomaticus minor	ZM	✓	x	x	x	x	a	a	a
AU12 Lip Corner Puller	Zygomaticus major	Z	✓	✓	✓	✓	✓	✓ (Zygomaticus)	✓	✓
AU13 Sharp Lip Puller	Levator anguli oris	LO	✓	x	x	x	x	x	a	✓ AU113 (Levator labii superioris alaeque nasi)
AUH13 Nostril lift	Levator annuli oris fascialis	LF	a	a	a	a	a	a	a	✓
AU14 Dimpler	Buccinator	B	✓	x	x	x	x	x	x	a
AU15 Lip Corner Depressor	Depressor anguli oris	DA	✓	x	x	x	x	x	a	a
AU16 Lower Lip Depressor	Depressor labii inferioris	DL	✓	✓	✓	✓	✓	✓ AU116 (Platysma)	✓	✓
AU17 Chin Raiser	Mentalis	M	✓	✓	✓	✓	✓	x	✓	✓
AU18 Lip Pucker	Incisivii labii, orbicularis oris	IL, OR	✓	a	✓	✓	✓	✓ AU118 (Orbicularis oris only)	✓ AU118 (Orbicularis oris, buccinator)	✓
AU20 Lip Stretch	Risorius	R	✓	x	a	a	a	a	a	a
AU21 Neck Tightener	Platysma myoides		✓	x	x	✓	x	a	a	a
AU22 Lip Fenneler	Orbicularis oris	OR	✓	✓	x	✓	✓	x	a	✓ AU122 Upper Lip Curler (Levator labii superioris, transverse nasi)
AU23 Lip Tightener	Orbicularis oris	OR	✓	x	x	x	x	x	a	a

AU24 Lip Presser	Orbicularis oris	OR	✓	✓	x	✓	✓	x	a	✓
AU25 Lips Parted	Despressor labii inferioris/levator labii superioris /orbicularis oris	DL/LS/ OR	✓	✓	✓	✓	✓	✓ (Orbicularis oris, caninus, LL: levator labii maxillaris, levator nasolabialis, platysma)	✓ (Orbicularis oris, caninus, LL: levator labii maxillaris, levator nasolabialis, platysma)	✓
AU26 Jaw Drop	Nonmimetic muscle		✓	✓	✓	✓	✓	✓	✓	✓
AU27 Mouth Stretch	Nonmimetic muscle		✓	✓	✓	✓	✓	✓	✓	✓ (Pterygoids, digastric)
AU28 Lips Suck	Orbicularis oris	OR	✓	✓	x	✓	✓	a	a	a
AU38 Nostril Dilator	Nasalis	NA	✓	x	x	x	x	a	a	a
AU39 Nostril Compressor	Depressor septi nasi, nasalis		✓	x	x	x	x	a	a	a
AU43 Eye Closure	Orbicularis oculi	OC	✓	✓	✓	✓	✓	✓	✓AU143 (Orbicularis oculi, retractor anguli oculi lateralis, levator palpebrae)	✓ AU143 (Orbicularis oculi, levator palpebrae superioris)
AU45 Blink	Orbicularis oculi	OC	✓	✓	✓	✓	✓	✓	✓ AU145 (Orbicularis oculi, retractor anguli oculi lateralis, levator palpebrae)	✓ AU145 (Orbicularis oculi, levator palpebrae superioris)
AU47 Half-blink	Orbicularis oculi, retractor anguli oculi lateralis, levator palpebrae (not on fig.)	OC, RO	a	a	a	a	a	a	✓	✓ (Orbicularis oculi)
AU200 Whiskers retractor	Lateralis nasi, orbicularis oris	LA,OR	a	a	a	a	a	a	✓ (Lateralis nasi, orbicularis oris)	a

AU201 Whiskers protractor	Caninus, orbicularis oris	CA,OR	a	a	a	a	a	a	✓ (Orbicularis oris, caninus)	a
AU202 Whiskers raiser	Lateralis nasi, caninus, orbicularis oris	LA, CA, OR	a	a	a	a	a	a	✓ (Orbicularis oris, caninus, lateralis nasi)	a

✓ = AU identified; x = AU not identified, but muscle present; a = AU not identified and muscle absent. Species-specific muscular variations are presented in brackets